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Genetic relationships between scrotal circumference and female reproductive traits[1]

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ABSTRACT: Records for yearling scrotal circumference (SC; n = 7,580), age at puberty in heifers (AP; n = 5,292), age at first calving (AFC; n = 4,835), and pregnancy, calving, or weaning status following the first breeding season (PR1, CR1, or WR1, respectively; n = 7,003) from 12 *Bos taurus* breeds collected at the Meat Animal Research Center (USDA) between 1978 and 1991 were used to estimate genetic parameters. Age at puberty (AP) was defined as age in days at first detected ovulatory estrus. Pregnancy (calving or weaning) status was scored as one for females conceiving (calving or weaning) given exposure during the breeding season and as zero otherwise. The final model for SC included fixed effects of age of dam at breeding (AD), year of breeding (Y), and breed (B) and age in days at measurement as a covariate. Fixed effects in models for AP and AFC were AD, Y, B, and month of birth. Fixed effects in models for PR1, CR1, and WR1 included AD, Y, and B. For all traits, random effects in the model were direct genetic, maternal genetic, maternal permanent environmental, and residual. Analyses for a three-trait animal model were carried out with SC, AP, and a third trait (the third trait was AFC, PR1, CR1, or WR1). A derivative-free restricted maximum likelihood algorithm was used to estimate the (co)variance components. Direct and maternal heritability estimates were 0.41 and 0.05 for SC; 0.16 and 0.03 for AP; 0.08 and 0.00 for AFC; 0.14 and 0.02 for PR1; 0.14 and 0.03 for CR1; and 0.12 and 0.01 for WR1. Genetic correlations between direct and maternal genetic effects within trait were −0.26, −0.63, −0.91, −0.79, −0.66, and −0.85 for SC, AP, AFC, PR1, CR1, and WR1, respectively. Direct genetic correlations between SC and AP and between those traits and AFC, PR1, CR1, and WR1 ranged from −0.15 (between SC and AP) to 0.23 (between AP and WR1). Estimates of heritability indicate that yearling SC should respond to direct selection better than AP, AFC, PR1, CR1, and WR1. Variation due to maternal genetic effects was small for all traits. No strong genetic correlations were detected between SC and female reproductive traits or between AP and the other female traits. These results suggest that genetic response in female reproductive traits through sire selection on yearling SC is not expected to be effective.

Key Words: Beef Cattle, Fertility, Heritability

Introduction

In general, only a small proportion of the variation for fertility traits in beef cattle can be accounted for by additive genetic variance (Lindley et al., 1958; Koots et al., 1994). Sire selection in beef cattle is an efficient method to achieve genetic progress because of the high selection intensity that can be applied on the male side. Among all measures of fertility in beef cattle, scrotal circumference (**SC**) presents several advantages. Scrotal circumference is easy and inexpensive to measure, has moderate heritability, and is reported to be favorably associated with female fertility (Brinks et al., 1978; Morris et al., 1992; Vargas et al., 1998). Positive genetic correlations between SC and growth traits (Bourdon and Brinks, 1986; Smith et al., 1989; Keeton et al., 1996) and between SC and semen quality traits (Neely et al., 1982; Knights et al., 1984; Smith et al., 1989) have been reported.

As a contribution to knowledge of genetic relationships of fertility traits between males and females, the objectives of this study were to estimate heritabilities for, and genetic correlations between, SC and age at

Table 1. Unadjusted means and standard deviations (SD), numbers of records, dams and sires for males with scrotal circumference measurements and females with measurements for five reproductive traits

Item	Records	Dams	Sires	Means (± SD)
Scrotal circumference, cm	7,580	4,519	714	32.59 ± 2.97
Age at puberty, d	5,292	3,462	576	356.16 ± 27.20
Age at first calving, d	4,835	3,328	583	713.19 ± 23.64
Pregnancy status following first breeding season[a]	7,003	4,349	625	0.75 ± 0.43
Calving status following first breeding season[a]	7,003	4,349	625	0.72 ± 0.45
Weaning status following first breeding season[a]	7,003	4,349	625	0.59 ± 0.49

[a]Coded as 0 for failure and 1 for success.

puberty in heifers (**AP**), and between SC and age at first calving (**AFC**), pregnancy status (**PR1**), calving status (**CR1**), and weaning status (**WR1**) for first-parity cows.

Materials and Methods

Data were collected from nine breeds (Hereford, **H**; Angus, **A**; Red Poll, **R**; Limousin, **L**; Simmental, **S**; Charolais, **C**; Pinzgauer, **P**; Gelbvieh, **G**; and Braunvieh, **B**) and three composite populations to which the nine pure breeds contributed (Meat Animal Research Center [**MARC**] I = ¼ B, ¼ C, ¼ L, ⅛ H, ⅛ A; MARC II = ¼ G, ¼ S, ¼ H, ¼ A and MARC III = ¼ R, ¼ P, ¼ H, ¼ A). The 12 breed groups were located at the U.S. MARC (USDA, ARS), Clay Center, NE. Their origins and management have been described by Gregory et al. (1991, 1992). The traits analyzed were: SC, AP, AFC, PR1, CR1, and WR1. Age at puberty was defined as age in days at the first detected ovulatory estrus. Scrotal circumference was measured (cm) in males at about 358 d of age. Pregnancy (calving or weaning) status in each year was coded as one if the female conceived (calved or weaned) given exposure during the breeding season and as zero otherwise. Data were collected from 1978 to 1991 and included 7,580 records for SC; 5,292 records for AP; 4,835 records for AFC, and 7,003 records for PR1, CR1, or WR1 following the first breeding season (Table 1).

Preliminary analyses were used (SAS Inst., Inc., Cary NC) to determine appropriate fixed effects for final mixed-model analyses. Different fixed effects (and corresponding interactions) were considered depending on the trait to be analyzed (Martinez-Velázquez, 2001). The final model for SC included fixed effects of age of dam (**AD**), year of birth (**Y**), breed (**B**), and age in days at measurement as a covariate (linear and quadratic). Fixed effects fitted to the models for AP and AFC were AD, Y, B, and month of birth. Fixed effects in models for PR1, CR1, and WR1 included age at breeding, year of breeding, and breed. Genetic parameters were estimated using a multiple-trait animal model (Henderson and Quaas, 1976). For all traits, random effects in the model were direct genetic, maternal genetic, maternal permanent environmental, and residual. The three-trait animal model was as follows:

$$
\begin{bmatrix} \mathbf{y_1} \\ \mathbf{y_2} \\ \mathbf{y_3} \end{bmatrix} = \begin{bmatrix} \mathbf{X_1} & 0 & 0 \\ 0 & \mathbf{X_2} & 0 \\ 0 & 0 & \mathbf{X_3} \end{bmatrix} \begin{bmatrix} \mathbf{b_1} \\ \mathbf{b_2} \\ \mathbf{b_3} \end{bmatrix} + \begin{bmatrix} \mathbf{Z_1} & 0 & 0 \\ 0 & \mathbf{Z_2} & 0 \\ 0 & 0 & \mathbf{Z_3} \end{bmatrix} \begin{bmatrix} \mathbf{g_1} \\ \mathbf{g_2} \\ \mathbf{g_3} \end{bmatrix} +
$$

$$
\begin{bmatrix} \mathbf{M_1} & 0 & 0 \\ 0 & \mathbf{M_2} & 0 \\ 0 & 0 & \mathbf{M_3} \end{bmatrix} \begin{bmatrix} \mathbf{m_1} \\ \mathbf{m_2} \\ \mathbf{m_3} \end{bmatrix} + \begin{bmatrix} \mathbf{W_1} & 0 & 0 \\ 0 & \mathbf{W_2} & 0 \\ 0 & 0 & \mathbf{W_3} \end{bmatrix} \begin{bmatrix} \mathbf{p_1} \\ \mathbf{p_2} \\ \mathbf{p_3} \end{bmatrix} + \begin{bmatrix} \mathbf{e_1} \\ \mathbf{e_2} \\ \mathbf{e_3} \end{bmatrix}
$$

where: $\mathbf{y_i}$ is the vector of observations for trait i, $\mathbf{b_i}$ is the vector of fixed effects for trait i, $\mathbf{g_i}$ is the vector of random additive genetic effects of animals for trait i, $\mathbf{m_i}$ and $\mathbf{p_i}$ are vectors of random maternal genetic and permanent environmental effects for trait i, $\mathbf{X_i}$, $\mathbf{Z_i}$, $\mathbf{M_i}$, and $\mathbf{W_i}$, are known incidence matrices relating the observations to fixed and random effects for trait i ($\mathbf{Z_i}$ and $\mathbf{M_i}$ were augmented with columns of zeroes for animals without records that were included in the relationship matrix), and $\mathbf{e_i}$ is a vector of random residual effects for trait i.

The first and second moments of the model are assumed to be:

$$
E\begin{bmatrix} \mathbf{y} \\ \mathbf{u} \\ \mathbf{p} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{Xb} \\ 0 \\ 0 \\ 0 \end{bmatrix} \text{ and } V\begin{bmatrix} \mathbf{u} \\ \mathbf{p} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{G_0} \otimes \mathbf{A} & & 0 \\ & \mathbf{P_0} \otimes \mathbf{I_p} & \\ 0 & & \mathbf{R_N} \end{bmatrix}
$$

where: $\mathbf{u} = [\mathbf{g'}\ \mathbf{m'}]'$ with $\mathbf{g'} = [\mathbf{g_1'}\ \mathbf{g_2'}\ \mathbf{g_3'}]$, $\mathbf{A}$ is the numerator relationship matrix, $\otimes$ is the right direct product operator, $\mathbf{G_0}$ is the additive-maternal genetic (co)variance matrix, $\mathbf{I_p}$ is an identity matrix with order the number of dams having progeny with records, $\mathbf{P_0}$ is a matrix of (co)variances among maternal permanent environmental effects for the three traits, and $\mathbf{R_N}$ is a matrix of residuals such that with only trait 1 or trait 2 or trait 3 measured, $\sigma_{e_1}^2$, $\sigma_{e_2}^2$, or $\sigma_{e_3}^2$ will be on the diagonal. With both traits 2 and 3 measured, $\sigma_{e_2}^2$ and $\sigma_{e_3}^2$ will be on diagonals and $\sigma_{e_2 e_3}$ will be on the corresponding off-diagonal, where $\sigma_{e_i}^2$ is the variance due to residual effects for trait i, and $\sigma_{e_i e_j}$ is the residual covariance for i^{th} and j^{th} traits measured on the same animal (i ≠ j). As implied below, the first trait is measured only on

Table 2. Estimates of phenotypic variance (σ_p^2), relative maternal permanent environmental variance (p^2), direct maternal genetic correlations within trait ($r_{d\text{-}m}$), and direct (h_d^2) and maternal (h_m^2) heritability (with SE for genetic parameters) for scrotal circumference and five female reproductive traits

Item	h_d^2	$r_{d\text{-}m}$	h_m^2	p^2	σ_p^2
Scrotal circumference	0.41 ± 0.04	−0.26 ± 0.42	0.05 ± 0.02	0.33	5.89
Age at puberty	0.16 ± 0.04	−0.63 ± 0.89	0.03 ± 0.02	0.03	373.96
Age at first calving	0.08 ± 0.04	−0.91 ± 0.95	0.00 ± 0.03	0.00	229.20
Pregnancy status following first breeding season	0.14 ± 0.03	−0.79 ± 0.71	0.02 ± 0.01	0.00	0.17
Calving status following first breeding season	0.14 ± 0.03	−0.66 ± 0.55	0.03 ± 0.01	0.00	0.18
Weaning status following first breeding season	0.12 ± 0.02	−0.85 ± 0.90	0.01 ± 0.01	0.00	0.22

males and traits 2 and 3 only on females. The covariances between residuals for traits measured on different sexes is assumed to be zero.

Estimates of the genetic parameters were obtained using a multiple trait derivative-free algorithm to obtain restricted maximum likelihood estimates (Boldman et al., 1995). No attempt was made to use a threshold model for PR1, CR1, or WR1 because the appropriate software to do two continuous and one binary trait was not available. However, some authors (Weller et al., 1988; Olesen et al., 1994; Matos et al., 1997) have reported no major differences between threshold and linear models in the genetic analyses of discrete traits. Analyses for a three-trait animal model were carried out with SC, AP, and a third trait (the third trait was AFC, PR1, CR1, or WR1). Starting values for the estimates of (co)variance components for the three-trait analyses were obtained from single- and two-trait analyses. Iterations were stopped when the variance of function values (−2 log L, with log L = logarithm of the likelihood given the data) of the simplex was less than the convergence criterion (1×10^{-6}). To check for convergence to a local rather than a global maximum, the analyses were restarted using the resulting estimates of the parameters as new starting values until the value of −2log L did not change in the first two decimal positions.

Results and Discussion

Heritability Estimates

Estimates of phenotypic variance (σ_p^2), proportion of variance due to maternal permanent environmental effects (p^2), and direct (h_d^2) and maternal (h_m^2) heritability for SC, AP, AFC, PR1, CR1, and WR1 are presented in Table 2. Among estimates of direct heritability, SC had the highest estimate (0.41) compared to estimates for AP (0.16), AFC (0.08), PR1 (0.14), CR1 (0.14), and WR1 (0.12). In general, SC has been reported to be moderately heritable in populations involving Zebu cattle with estimates of direct heritability ranging from 0.16 to 0.29 (e.g., Meyer et al., 1990; Kriese et al., 1991; Morris et al., 1992). In contrast, SC has been reported to be a highly heritable trait in *Bos taurus* populations, with estimates ranging from 0.36 to 0.71

(e.g., Latimer et al., 1982; Bourdon and Brinks, 1986; Morris and Wilson, 1997).

A relatively low estimate of direct heritability for AP (0.16) was obtained in the present study (Table 2). Similar estimates were found by Smith et al. (1989) for a population that included Hereford and Angus cattle and by Morris et al. (1993) for an Angus population (0.10 ± 0.17 and 0.15 ± 0.09, respectively). In contrast, several studies have reported higher estimates of heritability (from 0.27 ± 0.04 to 0.61 ± 0.17) for AP (e.g., MacNeil et al., 1984; Gregory et al., 1995; Morris et al., 2000).

In the present study, the estimate of direct heritability for AFC was 0.08 (Table 2). Similar estimates of heritability (0.01 ± 0.12 and 0.07 ± 0.09) were reported by Bourdon and Brinks (1982) and Smith et al. (1989), respectively. Several authors, however, have found higher estimates of direct heritability for AFC. Meacham and Notter (1987) reported a heritability estimate of 0.17 ± 0.04 for a Simmental population. Toelle and Robison (1985) and Buddenberg et al. (1990), working with data from Hereford herds, reported direct heritability estimates of 0.23 ± 0.11 and 0.39 ± 0.21, respectively.

Estimates of direct heritability for PR1, CR1, and WR1 on the binomial scale (0.14, 0.14, and 0.12 respectively) are presented in Table 2. In agreement with the estimate of h_d^2 for pregnancy status following the first breeding season (0.14) found in the present study, Evans et al. (1999) and Morris et al. (2000) reported heritability estimates of 0.13 ± 0.08 and 0.12 ± 0.05, respectively, for pregnancy rate of Hereford and Angus heifers. Lower estimates of direct heritability for pregnancy rate have been published by others. Toelle and Robison (1985) reported an estimate of 0.06 ± 0.06 for pregnancy rate of heifers in two Hereford herds. Morris and Cullen (1994) reported an estimate of 0.04 ± 0.04 for pregnancy rate of yearling females for a population, which included Hereford, Angus, and crossbred heifers. In contrast, a higher estimate of direct heritability (0.21 ± 0.12) was obtained for pregnancy rate of heifers in an Angus herd (Doyle et al., 2000).

Several authors have reported calving rate as a trait with low heritability. Dearborn et al., who (1973) analyzed data from first reproductive performance of crossbred heifers, reported an estimate of direct heritabil-

ity of 0.00 ± 0.01 for calves born live. A similar estimate (0.01 ± 0.02) was published for calving rate of heifers at 2 yr of age in a Hereford herd (Milagres et al., 1979). In contrast, the same study found a higher estimate (0.21 ± 0.13) when records of heifers that failed to calve at both 2 and 3 yr of age were excluded from the data. Splan et al. (1998) also reported different heritability estimates for calving rate of heifers depending on whether the estimate was expressed on an assumed underlying normal scale (0.19) or on the measured binomial scale (0.09 ± 0.04). Meyer at al. (1990), from an analysis of lifetime reproductive performance, reported pooled heritability estimates for calving rate on the binomial scale for Hereford (0.07), Angus (0.02), and Zebu (0.17) cattle.

In agreement with the estimate of direct heritability found in the present study for WR1, Koots et al. (1994) reported a weighted mean estimate of heritability of 0.17 ± 0.01 expressed on an underlying normal scale for percentage of calves weaned. In a different study, Dearborn et al. (1973) reported a heritability estimate of -0.01 ± 0.13 for percent calf crop weaned from an analysis of reproductive performance of crossbred females.

Estimates of direct heritability found for AP, AFC, PR1, CR1, and WR1 in the present study indicate that environmental and possibly nonadditive genetic sources of variation play major roles on the expression of those traits.

Maternal heritability estimates (Table 2) for all traits were small and ranged from 0.00 to 0.05. The estimate of maternal heritability found for SC (0.05) in the present study is less than the maternal heritability estimates reported by Kriese et al. (1991) for yearling SC for Hereford (0.12) and Brangus (0.10) bulls. No estimates of maternal heritability for AP, AFC, PR1, CR1, or WR1 were found in the literature. Results in Table 2 indicate that little variation in those traits is due to maternal genetic effects.

Estimates of Genetic Correlations

Estimates of direct maternal genetic correlations within trait for SC, AP, AFC, PR1, CR1, and WR1 are presented in Table 2. No previous estimates of direct maternal genetic correlations were found in the literature for AP, AFC, PR1, CR1, or WR1. In agreement with the estimate found for SC (−0.26) in the present study, Kriese et al. (1991) reported negative estimates of genetic correlation between direct and maternal genetic effects for yearling SC of Hereford (−0.24), and Brangus (−0.09) bulls.

Table 3 presents estimates of direct genetic correlations (r_{d-d}) between SC and AP and between those traits and AFC, PR1, CR1, and WR1. A small but favorable estimate of r_{d-d} between SC and AP (−0.15) was found in the present study. Other authors have agreed that a favorable genetic relationship exists between SC and AP, but those authors have reported estimates that indicate a stronger genetic association. Morris and Wilson (1997) and Morris et al. (2000) found direct genetic correlations of −0.30 and −0.25, respectively, between SC and AP. Morris et al. (1992) working with Hereford, Angus, and crossbred cattle, and Vargas et al. (1998) using data from a Brahman herd, reported genetic correlations of −0.39 and −0.32, respectively, between the same two traits. Morris et al. (1993) analyzing an average measurement of SC estimated a direct genetic correlation of −0.81 between SC and AP in an Angus herd. A similar estimate (−0.71) was published by Brinks et al. (1978). In agreement with those results, Moser et al. (1996) concluded that Limousin bulls with high yearling SC EPD could be expected to produce daughters reaching puberty at significantly earlier ages. In contrast, Smith et al. (1989) and Perry et al. (1990) reported nonsignificant relationships ($P > 0.05$) between age at puberty in heifers and SC of yearling males.

An unfavorable but small estimate of direct genetic correlation of 0.15 was found in the present study between SC and AFC (Table 3). Toelle and Robison (1985) reported a large unfavorable estimate of genetic correlation (0.58) between yearling SC and AFC of heifers calving at 2 yr of age from a sire-daughter analysis. However, in the same study with paternal half-sib analyses, favorable estimates of r_{d-d} were reported for the analyses that included AFC of heifers calving at 2 yrs of age (−0.14) or of heifers producing the first calf at either 2 or 3 yr of age (−0.38). A favorable but nonsignificant ($P > 0.05$) partial regression coefficient of AFC of heifers on yearling SC of their sires (−0.826 d/cm) was reported by Smith et al. (1989).

As can be seen in Table 3, negligible estimates of genetic relationship were detected between SC and PR1. This result agrees with the estimate published by Evans et al. (1999), who reported a direct genetic correlation of 0.002 ± 0.45 between the two traits. Similarly, Kastelic et al. (1996) reported a near-zero relationship between SC and pregnancy rate of Angus heifers. Others have published favorable genetic correlations between those two traits. Toelle and Robison (1985) found genetic correlations of 0.26 (half-sib analysis) and 0.93 (sire-daughter analysis) between yearling SC and pregnancy rate of heifers. Morris and Cullen (1994), with an average measurement of SC, estimated direct genetic correlations between SC and pregnancy rate of yearling heifers to be 0.53 ± 0.66 and between SC and lifetime pregnancy rate to be 0.34 ± 0.40 in Angus cattle. Smaller but favorable estimates were reported by Morris et al. (2000), who published estimates of genetic correlations between SC and pregnancy rate of yearling heifers (0.14 ± 0.14), between SC and pregnancy rate of 2-yr-old females (0.25 ± 0.26), and between SC and pregnancy rate of cows (0.07 ± 0.23). However, in the same study, the authors reported an unfavorable estimate of genetic correlation between SC and mean pregnancy rate (-0.12 ± 0.20) for cows mated at 3 yr of age or older. An unfavorable

Table 3. Estimates of direct (r_{d-d}) and direct-maternal (r_{d-m}) genetic correlations between scrotal circumference (SC) and age at puberty (AP) and between those traits and age at first calving (AFC), pregnancy status following first breeding season (PR1), calving status following first breeding season (CR1), and weaning status following first breeding season (WR1)

Item		SC	AP	AFC	PR1	CR1	WR1
Scrotal circumference	r_{d-d}		−0.15[a]	0.15	0.00	0.00	0.00
	r_{d-m}		−0.28[a]	0.25	0.12	0.00	0.00
Age at puberty	r_{d-d}	−0.15[a]		0.00	0.00	0.08	0.23
	r_{d-m}	0.10[a]		0.00	−0.06	0.00	−0.01
Age at first calving	r_{d-d}	0.15	0.00		—	—	—
	r_{d-m}	0.01	−0.23		—	—	—
Pregnancy status following first breeding season	r_{d-d}	0.00	0.00	—		—	—
	r_{d-m}	0.00	0.00	—		—	—
Calving status following first breeding season	r_{d-d}	0.00	0.08	—	—		—
	r_{d-m}	0.00	0.00	—	—		—
Weaning status following first breeding season	r_{d-d}	0.00	0.23	—	—	—	
	r_{d-m}	0.00	−0.01	—	—	—	

[a]Average from the four, three-trait analyses with SC and AP.

estimate of genetic correlation was also found between yearling SC and lifetime pregnancy rate (−0.25) in a composite beef herd (Mwansa et al., 2000).

Near-zero estimates of additive genetic correlations were found between SC and CR1 and between SC and WR1 (Table 3). No estimates of direct genetic correlations between those traits were found in the literature.

Estimates of r_{d-d} between AP and AFC (or PR1, CR1, or WR1) are presented in Table 3. Near-zero estimates of additive genetic correlations were found between AP and AFC and between AP and PR1. Low estimates of genetic correlations were found between AP and CR1 (0.08) and between AP and WR1 (0.23). In contrast, Morris and Cullen (1994) reported favorable genetic correlations for age at first estrus and yearling pregnancy rate (−0.30 ± 0.26) and between age at first estrus and lifetime pregnancy rate (0.29 ± 0.26). Similarly, favorable genetic correlations for standardized age at first estrus with yearling pregnancy rate (−0.89 ± 0.17) and with pregnancy rate of 2-yr-old females (−0.29 ± 0.30) were published by Morris et al. (2000). In another study, Mwansa et al. (2000) reported a low estimate of genetic correlation between AP and lifetime pregnancy rate (−0.21) for a composite beef cattle population. Earlier, Laster et al. (1979) reported correlations based on breed group means between AP and percentage pregnant (−0.42) and between AP and heifers calving at 2 yr of age during the first 25 d of the calving season (−0.75). Similarly, Doornbos et al. (1983) detected a favorable residual correlation (−0.42) between age at puberty and percentage pregnant in Hereford heifers. Estimates of r_{d-d} between AP and pregnancy status between this and previous studies would be expected to be different because of differences in populations and management systems. Favorable estimates were found in the literature, but in general, those estimates also had large standard errors. No estimates of direct genetic correlations between AP

and CR1 or between AP and WR1 were found in the literature. Table 3 summarizes estimates of direct maternal genetic correlations between traits. Low estimates were obtained, suggesting that genetic links between direct and maternal genetic effects of different traits are negligible.

In general, estimates of heritabilities and genetic correlations from the present and other studies are variable. One possible reason could be that estimates from early papers were obtained from regression or ANOVA methods based on sib covariances (Lindley et al., 1958; Brinks et al., 1978; Toelle and Robison, 1985) The variance components obtained by those methods could be biased, mainly due to parents not being a random sample of the population studied. In contrast, the REML method used in the present and other recent studies (e.g., Meyer et al., 1990, 1991; Morris et al., 1992, 1993, 2000; Vargas et al., 1998) accounts for selection of parents. The REML method may better adjust observations for the fixed effects. Other reasons for discrepancies among estimates of genetic parameters could be related to models used in the classical experiments (sire model) compared to more recent analyses (animal model), or to differences among populations (different breeds, management systems, environments) from which data were obtained.

Implications

Estimates of heritability indicate that yearling scrotal circumference should respond to direct selection better than age at puberty, age at first calving, and first parity pregnancy, calving, and weaning rates. The low estimates of maternal heritability indicate that variation due to maternal genetic effects is negligible for all the traits. No strong genetic correlations were detected between scrotal circumference and female reproductive traits or between age at puberty and the

other female traits. In certain populations and management systems, such as the Germ Plasm Utilization program, genetic response in female reproductive traits by selecting sires on yearling scrotal circumference (or age at puberty in heifers) may be expected to be less effective than previously reported in the literature.

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